The Eye of Peripatus.

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With Plate 7 and 3 Text-figures.

THE first description of the minute structure of the Eye of Peripatus was given by Balfour (**1**) in his memorable paper on the anatomy of Peripatus capensis. So far as I am aware nothing has been added to our knowledge of the structure since that date, despite the advances in microscopical technique, and the rather thorough investigation of invertebrate visual organs. Other arthropod eyes have received considerable attention, and this seems strange at first because a comparison of the Peripatus eye with that of other arthropods should be highly interesting by reason of the phyletic position occupied by the Onychophora.

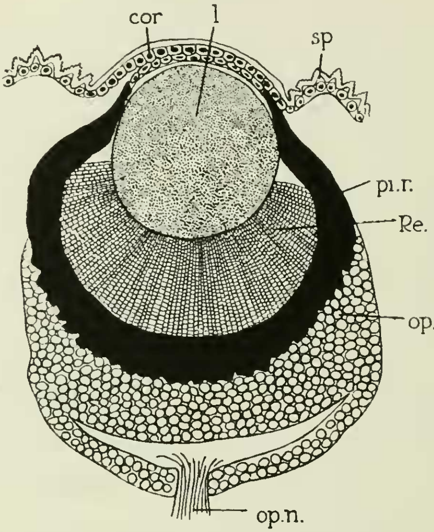
The development of the eye was followed by Sedgwick (**4**), but nothing was added to the previous knowledge of the structure of the adult eye, although the origin of the different parts was very clearly shown.

In Balfour's illustration, the structure of the eye of Peripatus capensis is shown in longitudinal section through the head. This figure has been often recopied, and it will be well to take note of the details brought out (see Text-fig. 1, which is a copy of that after Balfour in this Journal, vol. 23). The general cuticle of the body wall is continued as a thin layer over the eye. Below this is the cornea—a layer of epithelial cells, which are continuous with the epidermis. Between the cornea and the lens there is another cell layer which appears to terminate peripherally against the region marked pigment. There is no evidence to show that the structures masked by the pigment were ever brought to light.

From the illustration it would appear as if the pigment formed a separate layer which acted as a kind of capsule enclosing the retina and bounding the eye internally. This impression is strengthened by the fact that the cells below the pigment are marked ' optic ganglion '.

The space within the structures enumerated above is occupied by the lens, and by a layer termed the rods.

Text-fig. 1.



Longitudinal section of the Eye of Peripatus capensis after Balfour, ' Quart. Jour. Micr. Sc.', vol. 23, plate 18, fig. 24. *cor.* = cornea; *l.* = lens; *op.* = optic ganglion; *op.n.* = optic nerve; *pi.r.* = pigment; *Re.* = rods; *s.p.* = secondary papilla.

Now let us turn to the results of the present investigation. The species utilized was Peripatoides occidentalis from Western Australia. A large number of preparations had to be made, including sections and maceration preparations. No single method can be singled out, the usual series of fixatives and stains must be adopted, one method giving a little information, another a little more (see Dakin, " Eye of Pecten ", ' Quart. Journ. Micros. Sci.', 1909).

The Eye of Peripatus is not stalked although the distal surface forms a dome-shaped protuberance on the skin. The whole of this bulge appears to be occupied by the lens. In sections which have not been depigmented (see left side of fig. 1) the eye appears to be made up of three regions—the lens, the region previously known as the retina (or rod region), and the so-called optic ganglion. Now it will clear matters up at once if we state that the rod layer does not consist of cells but only of parts of cells—i. e. the distal halves of cells whose nuclei lie internally to the pigment. In other words, the so-called optic ganglion plus the rod layer together make up the retina. The units of these layers are not separated by a layer of pigment ; the pigment is actually enclosed within the cells (see fig. 2).

The Cuticle overlying the eye (fig. 1, *Cut.*) differs from that of the surrounding regions in being free from the small projections so characteristic elsewhere. Not only are the minute spines absent, but the dermal papillae which are present over the entire body wall are missing here.

The Epidermis is continued over the eye to from the Cornea (fig. 1, *Cor.*). Most of the cells of the general epidermis are somewhat cubical or pyramidal in form, with large nuclei. The corneal cells are very different, being quite flat. The nuclei are decidedly compressed and the protoplasm is reduced in amount.

The Subcorneal layer of cells may be said to form a capsule which encloses the lens. It is seen as a well-marked layer where it covers the lens and extends down over the rod layer (fig. 1, *Sub. Cor.*). There is nothing of importance to add further regarding it except that in the development of the eye it formed the outer portion of a complete vesicle, the proximal cells of which have given rise to the retina (see fig. 5).

The Lens is non-cellular and forms a homogeneous mass which stains readily with eosin. The face towards the retina appears almost flat in well-preserved sections, whilst the distal surface is highly convex, so that the entire structure is practically a dome. In all the well-preserved sections the proximal surface of the lens was in contact with the face of the retina. A delicate non-nucleated sheath appears to bound the lens, but it is in all probability only the outermost layer of the lens substance.

The Structure of the Retina.

Very little trouble will suffice to show quite clearly the structure of the dioptrical part of the eye described above. The elucidation of the structure of the retina is a much more difficult task, and it is quite natural that this essential part of the eye has remained misunderstood.

As we have already seen, the pigment band does not enclose the retina, but is made up of pigment granules lying within the retinal elements. We shall keep the term Rods for the real constituents of the rod layer, the part marked *Re.* in Balfour's figure. This rod layer in poor, or even in moderately good sections, appears to be made up of rather long 'rods' separated by clear spaces. The 'rods' also have a peculiar broken-up appearance even when not cut obliquely, as appears most frequently to have been the case. Now as a matter of fact these dark-staining bodies are not the rods. Maceration preparations, but still more certain, transverse sections in the plane of the retina, show quite clearly that the rod layer is not exactly what it seems. It comes as a surprise, in fact, to discover that the dark-staining part of the rod layer appears in transverse sections as a grating or net (see fig. 3). It now requires the study of depigmented longitudinal sections and maceration preparations to explain the above. Really the explanation is simple. The retina is built up of one kind of unit only, and there are no supporting cells or other non-visual elements. Each visual unit consists of a rod-cell bearing a rod.

The Rod-cells and Rods. A rod-cell (see fig. 2, and fig. 1, *Rod-cell*) consists of a columnar portion containing finely-granular protoplasm and crowded with pigment granules, and a proximal constricted and unpigmented part swollen out by the nucleus. As the rod-cells are numerous and the nuclei rather large, the latter are arranged at different levels in the cells. It is the nuclei of the rod-cells which collectively have been mistaken for an optic ganglion.

Proximally the rod-cells are continued as nerve fibres, which form the very short optic nerve. The distal portions of the rod-cells are hexagonal in section, so that all fit together closely to form a mosaic (fig. 4).

The rods are projections from the rod-cells, but the main part, the axis, of the rod is composed of a rather non-staining material. Thus in longitudinal sections the axes of the rods lie between the stained column-like bodies, whilst in transverse sections the rods would be the meshes of the grating (see fig. 3). The next question is, naturally, what is the 'grating' itself, the part so easily mistaken for the rods in longitudinal section. It would appear as if this staining substance was simply the peripheral portions of the rods.

Each rod can be seen in maceration preparations to bear peripheral 'Stiftchen'—short processes very characteristic of invertebrate visual cells. These 'Stiftchen' clothe each rod completely, and it is the 'Stiftchen', or the 'Stiftchen'-borders, of the rods which stain up so readily and actually appear to be the rods in longitudinal sections. This explains why they show up as a kind of grating when cut transversely, for the 'Stiftchen'-borders of adjacent rods touch each other (see figs. 1 and 3).

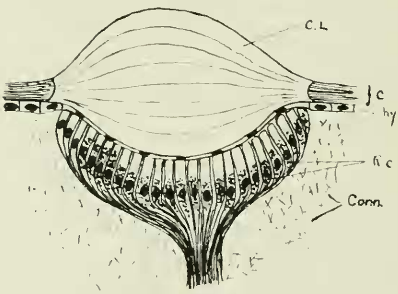
Underlying the layer of rod-cells is a collecting region of nerve fibres—the prolongations of the sensory cells. These collect to form a short optic nerve (fig. 1, *Op. N.*) which enters the brain. The optic tract is traceable for some distance within the 'Punktsubstanz'. A delicate layer of connective tissue forms a capsule bounding both retina and optic nerve.

Comparison of the Eye of Peripatus with that of other Arthropods, and with the Polychaete Eye.

The Eye of Peripatus is in reality a very simple structure compared with some insect ocelli. It is developed, as was discovered by Sedgwick (**4**), as a simple vesicular invagination of the ectoderm. The vesicle cut off gives rise to the subcorneal layer and the retina (see fig. 5). The lens is secreted within this vesicle and is non-cellular. It has no connexion directly with the cuticle of the body-wall, nor is the latter thickened as it passes over the cornea.

The description already given shows clearly that we can exclude the complicated compound eyes of the Insects and Crustacea so far as our comparison is concerned. No information regarding the origin of the compound eye of the arthropoda is likely to be obtained by the study of the Eye of Peripatus. Comparison must be made, then, with the lower and more

TEXT-FIG. 2.



Insect ocellus (Helophilus) after Hesse, somewhat modified. *C.* = cuticle; *C.L.* = cutic. lens; *Conn.* = connective tissue; *hy.* = hypodermis; *R.c.* = rod-cells of retina. Note difference in character of lens from that of Peripatus. The formation of lens by thickening of cuticle over eye is very characteristic in Insecta.

simple arthropod visual organs, the simple eyes. We shall also exclude the Arachnoid eyes, the structure of which (see Lankester (**6**), and Watase) is again different in type. We are left with the Myriapod eyes and the larval eyes and ocelli of insects.

A marked difference is easily recognized between the Eye of Peripatus and the above. In the ocelli of insects (Helophilus, Ceratopsyllus, &c., see Text-fig. 2) and in the larval eyes, we usually find that the ectoderm is invaginated to form the retina (see literature **2** and **3**). We do not find a complete vesicle. The ectoderm does not give rise to a completely separated vesicle, part of which becomes a subcorneal layer. On the other hand the retinal layer can be traced into the ectoderm.

With this marked difference we must also note that the lens in the Insecta and the Myriapoda is directly continuous with the cuticle and is indeed a local thickening of the same, whilst in Peripatus it is secreted within the vesicle.

The modern work confirms, therefore, the statements of Lankester (**5**), when in his article on the structure and classification of the Arthropoda he adds, '. . . the Chaetopod eye, which is found only in the Onychophora where the true Arthropod eye is absent. The essential difference between these two kinds of eye appears to be that the Chaetopod eye (in its higher developments) is a vesicle enclosing the lens, whereas the Arthropod eye is a pit or series of pits into which the heavy chitinous cuticle dips and enlarges knobwise as a lens'.

Thus whilst we can homologize the cuticle, cornea, subcorneal layer, &c., of Peripatus with parts of the simple eyes of the Myriapoda and Insecta, the Peripatus eye is not primitive so far as the dioptrical parts are concerned, but has developed along its own lines and resembles that of the highly-developed Chaetopoda. The Eye of Peripatus has, however, not evolved very far, and its retina is quite simple and indeed not at all unlike that of the median ocelli of Helophilus (one of the Diptera) or of the eye of Scolopendra. In both these examples we have retinas consisting solely of visual cells. These cells bear rods which are remarkably like those of Peripatus and have the same marginal (lateral) 'Stiftchensaum'. Indeed, the rods of the Scolopendra retina stain very like those of Peripatus.

Hesse speaks of the retinal elements of these eyes as being of a very original type. It is particularly interesting, therefore, to find the agreement with Peripatus.

The histology of the Polychaete eye has been investigated in some detail by R. Hesse (**3**). We can find material for comparison in his papers.

Eyes are to be found of very varying form and complexity of development. In a great many cases an open cup-shaped retina is to be seen (resulting from ectodermal invagination), but there is no lens, cuticular or otherwise. The retina in nearly all cases consists of rod-cells bearing rods which are directed distally. In a large number of the eyes, the histology of which has been investigated, the details are not very similar to the Eye of Peripatus. Hesse's figure of the eye of Siphonostomum diplochaetos is, however, curiously like that of the early illustrations of the Peripatus eye so far as the retina

TEXT-FIG. 3.

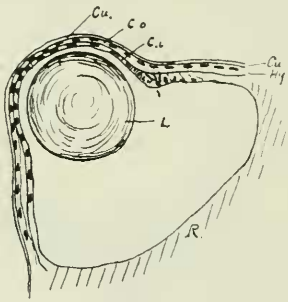


Diagram of lens and corneal layers of eye of Polychaete (Vanadis formosa), modified after Hesse. Note similarity of arrangement of layers to that found in Peripatus. *C.o.* = outer cornea; *C.i.* = inner cornea; *Cu.* = cuticle; *Hy.* = hypodermis; *L.* = lens; *R.* = retina (structure not shown).

is concerned. Both the vertical sections and those taken in the plane of the retina indicate this, and no doubt the structure is almost exactly the same as that of the Eye of Peripatus. A detailed re-examination with up-to-date methods would be necessary to make it certain.

The remaining features (dioptrical) of this Polychaete eye are quite unlike those of Peripatus. The eye is not nearly so well developed as that of the latter.

One of the best-developed Polychaete eyes is found in the group Alciopidae. We have here a vesicular eye (see Text-fig. 3) with enclosed and well-developed lens. There are many resemblances to the Eye of Peripatus. The cuticle, for example, is continued over the eye without thickening. Below this, and between it and the lens, there are two cellular layers—an outer cornea and an inner cornea. These correspond exactly to the corneal and subcorneal layers in Peripatus. The lens is non-cellular.

We need not carry our comparisons further; they may be summed up as follows: (1) The retina of the Eye of Peripatus is of a simple and primitive type, and is found again in the ocelli of certain Diptera and in the eyes of some Myriapoda. It is also not unlike that of some Polychaeta. (2) The dioptrical parts of the Eye of Peripatus (lens and corneal layers) are well developed and, as pointed out by Lankester, are arranged in a manner quite unlike that met with in the Diptera, Myriapoda, or Crustacea. These parts, on the other hand, resemble very closely the similar structures of the Polychaete Vanadis. (3) The Eye of Peripatus possesses some features of a simple type met with in other Arthropod groups and in the Polychaeta, but so far as the Arthropoda are concerned it has followed its own line of evolution and remains quite distinct.

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EXPLANATION OF PLATE 7.

Illustrating Prof. W. J. Dakin's paper on 'The Eye of Peripatus'.

Fig. 1.—The Eye of Peripatoides occidentalis in vertical section (longitudinal through the eye). The right half of the retina is represented in the depigmented condition, the left side in the natural state. × 740. *Cor.* = cornea; *Cut.* = cuticle; *Sub. Cor.* = subcorneal layer; *Op. N.* = optic nerve; *Epid.* = epidermis; *Mus.* = muscle-cells; *L.* = lens.

Fig. 2.—Complete rod-cell with rod isolated from the retina. Maceration preparation. × 1,500. *Pig.* = pigment; *Nuc.* = nucleus of rod-cell.

Fig. 3.—Transverse section through retina in plane of the rods (stained haematoxylin, Ehrlich). × 1,500.

Fig. 4.—Transverse section through retina, in plane of rod-cells in the region where pigment is present. (Depigmented section.) × 1,500.

Fig. 5.—Diagrams illustrating the development of the Eye of Peripatus.

(*a*) Invagination of ectoderm.

(*b*) Invagination of ectoderm complete.

(*c*) Ectodermal vesicle cut off.

(*d*) Proximal cells give rise to retina, the distal becomes the subcorneal layer.

(*e*) Retina developed, lens secreted by cells of vesicle.